

A NEW SPECIES OF *AQUARIUS* (HETEROPTERA: GERRIDAE) FROM TIMOR,  
WITH NOTES ON TIMORESE ZOOGEOGRAPHY

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*Abstract.*—*Aquarius lili* n. sp. is described from western Timor, and compared with other species in the genus, with figures of the male and female abdominal terminalia and genital structures provided. On the basis of the characters used by Andersen (1990) to produce a species level phylogeny for the genus, this new species is a member of the *paludum* group, and is most closely related to *A. adelaidis* (Dohrn), a species occurring from India to Borneo. The oddly disjunct distribution of this Timorese species and its zoogeographic implications in regard to competing geological hypotheses concerning the tectonic evolution of the island are discussed.

*Key Words:* *Aquarius*, Timor, taxonomy, zoogeography

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The genus *Aquarius* Schellenberg was recently revised by Andersen (1990), who recognized 15 species. These taxa are chiefly Holarctic with only five widely disjunct species known from the Southern Hemisphere. Our discovery of a new species from Timor that conforms to Andersen's (1990: 45) diagnosis of *Aquarius* is of interest, because it adds yet another geographically restricted Southern Hemisphere form to the latter assemblage.

The *Aquarius* species occurring in nearest geographical proximity to the new Timorese species are *A. fabricii* Andersen from Northwest Australia and *A. adelaidis* (Dohrn) from the western Malay Archipelago (Fig. 5). *Aquarius adelaidis* was previously reported from Sumatra and Luzon, and we now have a record from Borneo based on a single female specimen from the following locality: Indonesia, Kalimantan Timur Province, stream 4 km. NE of Kota Bangun on the Samarinda road, 29 August 1985, CL 2097, D. A. and J. T. Polhemus (BPBM). The genus *Aquarius* was also listed

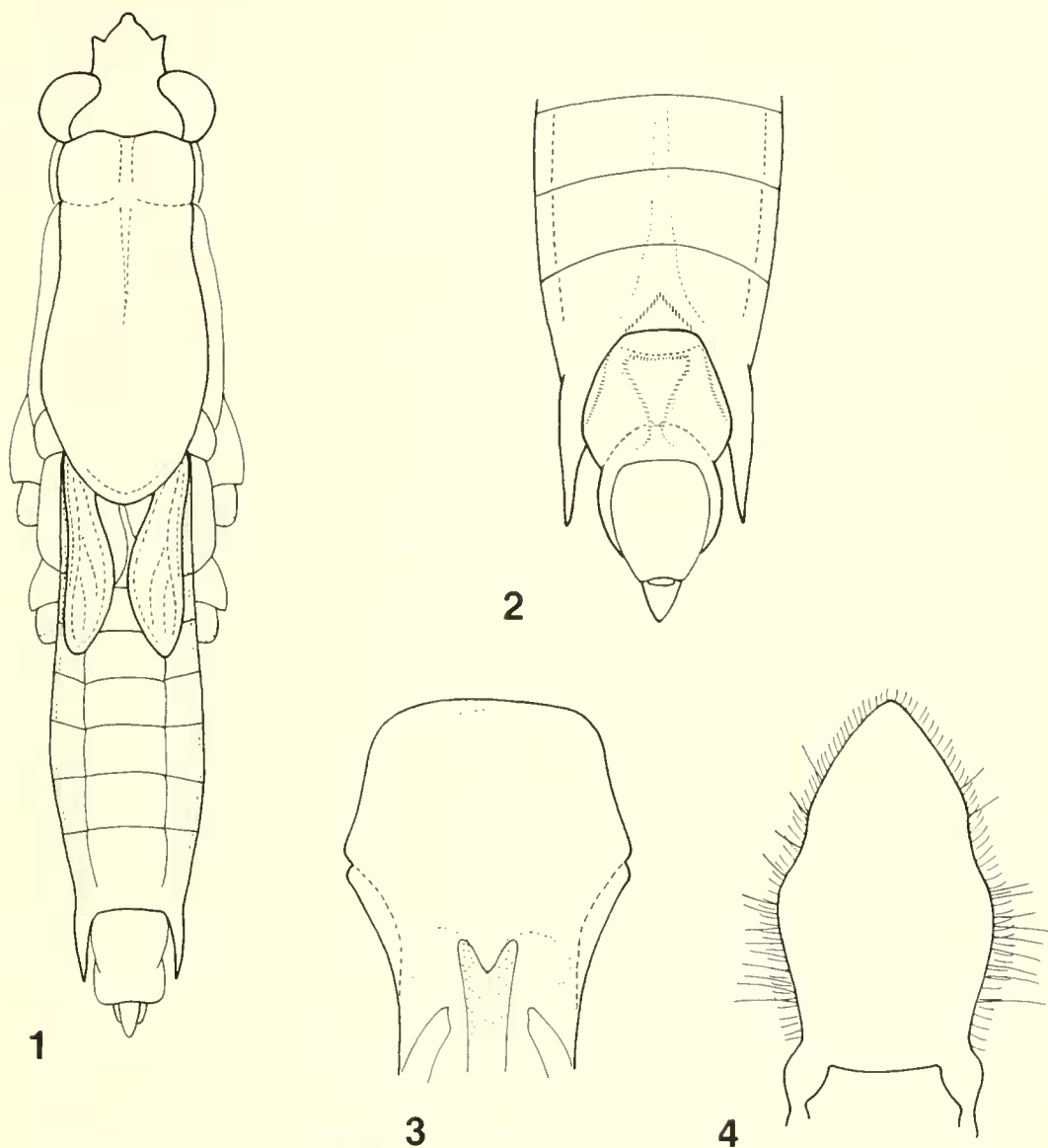
as occurring on Celebes by Polhemus and Polhemus (1990, table 1), but this was an error, and as correctly pointed out by Chen and Nieser (1992), the genus is in fact unknown from that island.

*Aquarius lili*, NEW SPECIES

Figs. 1-4

*Diagnosis.*—*Aquarius lili* is clearly a member of the *paludum* group as defined by Andersen (1990: 44). It is most closely allied to *A. adelaidis* Dohrn, but differs in having shorter antennae, a weakly instead of strongly V-shaped emargination on male ventrite VII, shorter connexival spines, and the female proctiger angulate distally instead of rounded. The male genitalia of *A. lili* are closest to *adelaidis*, but the dorsal plate is not as highly sinuate distally (Fig. 3). The sclerites of the aedeagus are very similar to those illustrated for *adelaidis* by Andersen (1990) and Miyamoto (1967).

In Andersen's (1990) key, *lili* does not run satisfactorily to any species; difficulties develop with couplet 3, because *lili* is bra-



Figs. 1-4. *Aquarius lili* n. sp. 1, Male, dorsal habitus (legs omitted). 2, Male terminal abdomen, ventral view. 3, Distal part of male phallic vesica, dorsal view. 4, Male proctiger.

chrypterous, yet the male connexival spines do not surpass the caudal margin of segment VIII. On the basis of the connexival spines, *lili* proceeds to couplet 4, then to couplet 11, where it matches neither of the Australian species, *fabricii* or *antigone*. If forced to couplet 12, *lili* immediately fails, because the hind femora are much longer than the

mid femora, yet male ventrite VII is roundly emarginate or nearly so (i.e. weakly V-shaped).

Description (all measurements in millimeters).—*Brachypterous male*: Length, mean 10.25 (N = 2, min. 10.0, max. 10.5); width, mean 2.72 (N = 2, min. 2.66, max. 2.77) (Fig. 1). Ground color blackish, cov-

ered with fine golden pubescence; mesopleura set with longer setae; head with chevron shaped brownish yellow mark posteriorly on vertex. Pronotum with brownish yellow median stripe the length of anterior lobe; posterior lobe margined with yellowish, more broadly caudad; acetabulae beneath, venter of prothorax, venter of head anteriorly, basal two rostral segments, anterior trochanters, anterior femora basally, caudal extreme of abdomen, and connexival margins leucine tinged with fuscous. Middle and hind trochanters, femora basally brownish. Legs and antennae black.

Length of head (1.28) about double narrowest interocular space (0.67); width of eye 0.67; eyes extending posteriorly about  $\frac{1}{2}$  length of propleura. Rostrum short, reaching between anterior coxae. Antennae long, all segments of about equal diameter, length of segments I–IV: 1.55; 0.89; 0.67; 1.00; all antennal segments without stout spines, segment IV bearing 5–6 slender setae of length about  $\frac{1}{2}$  width of segment.

Pronotum long (4.00), narrow (1.72), anterior margin slightly sinuate, distinctly elevated behind eyes; posterior margin broadly rounded, yellowish margin slightly raised; anterior lobe sharply demarcated from posterior lobe; posterior lobe with weak longitudinal median carina, humeri not pronounced. Wing rudiments orange brown, reaching onto tergite III, venation reduced but distinct; metasternum medially with a large patch of dense appressed setae, appearing golden brown in oblique light.

Abdominal tergites II–VI about of equal length (0.44–0.55), tergite VII longer (0.92); VIII long (0.92), large; proctiger triangular in dorsal view, ventrally tumid basally, caudally carinate; male terminalia as shown in Figs. 2–4. Connexiva moderately raised, spines reaching  $\frac{2}{3}$  to tip of tergite VIII. Posterior margin of sternite VII shallowly and roundly emarginate, with hint of V-shape medially (Fig. 2).

Anterior femur thickened, not flattened ventrally, postero-distally with a stout spur;

anterior tibia slightly widened distally; middle femur with distal spur. Measurements of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 3.88: 2.89: 0.44: 0.55; of middle leg, 10.65: 7.88: 1.78: 0.67; of hind leg, 11.76: 6.38: 1.83: 0.72; anterior femur unmodified, with fine dense appressed pile ventrally; middle and hind femora, tibia thickly set with minute black spines.

Proctiger elongate, coming to a rounded acute tip (Fig. 4). Vesica with dorsal plate produced, distally widened, margins weakly sinuate (Fig. 3).

*Brachypterous female:* Coloration as in male, but body more robust. Length, mean 11.63 (N = 6, min. 11.0, max. 12.2); width, mean 2.91 (N = 6, 2.83, max. 3.00). Proctiger rounded posteriorly.

*Macropterous male:* Similar to brachypterous form in most respects; length, mean 11.0 (N = 3, min. 10.7, max. 11.3); width, mean 2.73 (N = 3, min. 2.66, max. 2.83). Pronotum with posterior lobe more raised, humeri more prominent. Wings light brown, veins blackish brown, set with bright golden pubescence, reaching beyond tip of abdomen.

*Macropterous female:* Similar to brachypterous form in most respects, except wings exceeding tip of abdomen; length, mean 12.4 (N = 1); width, mean 3.05 (N = 1).

Etymology.—The name *lili* refers to the Lili River type locality.

Ecological notes.—The Lili River at the type locality was a relatively shallow stream flowing in an unshaded bed of rocks, cobbles and gravels. The stream profile consisted of shallow riffles connecting deeper rock rimmed pools, and it was on these pools that *A. lili* occurred most abundantly. At Baumata spring this species was found on the large, deep pool formed at the spring head, with individuals skating on deep, open waters far from shore where they were difficult to capture.

Material examined.—Holotype, brachy-

pterous male and allotype, brachypterous female: INDONESIA, Timor, Nusa Tenggara Timur Prov., Lili river at Lili, nr. Camplong, 40 km E. of Kupang, 65 m., water temp. 32° C, CL 2592, 11 September 1991, J. T. & D. A. Polhemus (USNM).

*Paratypes as follows:* INDONESIA, Timor, Nusa Tenggara Timur Prov.: 3 brachypterous males, 3 macropterous males, 7 brachypterous females, 5 macropterous females, 1 nymph, same data as holotype (JTFC, BPBM, MZB); 2 macropterous females, spring and outflow streams at Baumata, 17 km. E. of Kupang, 215 m., water temp. 30° C., 10 September 1991, CL 2590, D. A. and J. T. Polhemus (JTFC).

#### PHYLOGENY

The phylogenetic analysis of *Aquarius* presented by Andersen (1990) is the foundation for the phylogenetic interpretation proposed here, which focuses on the *paludum* species group. Our cladistic analysis utilizes Andersen's (1990) data set insofar as possible (see Appendix 1), but certain apomorphic states given in his Table 1 could not be coded properly for *A. lili* without modification or reinterpretation as follows; the character as described by Andersen is given first, followed by comments:

Character 20.—Posterior margin of male sternum 7 concave and with an angular emargination in the middle.

*Comments:* For *A. adelaidis* (Dohrn), *A. distanti* (Horvath) and *A. paludum* (Fabricius) in the *paludum* group, this character should be coded +, but for *lili* it should be coded -. The V-shaped emargination is strongest in *distanti*, and weaker but definitely present in the other species, except for *lili*, in which it is barely developed.

Character 22.—Fore femora uniformly dark.

*Comments:* Many species of *Aquarius* have at least the base of the fore femora with light colored streaks, and often the distal part as well. This character should either be redefined as "fore femora mostly dark;

light markings restricted to basal and distal extremes," or discarded. If written as above, it will hold for the *paludum* group and most other species, but not all. Specimens of *A. amplus* (Drake & Harris) have the fore femur uniformly brown, and specimens presently considered to be *A. remigis* (Say) from Arizona and Mexico have the fore femora brown with black longitudinal streaks. Some specimens of *A. cinereus* from Algeria have a light colored fore femur with black longitudinal stripes similar to many species of *Gerris*.

Despite these differences in character interpretation, we did not find these changes to alter the placement or relationships of the terminal taxa on the tree, which was our primary concern. When character states for *A. lili* were coded using Andersen's original set of 39 characters, subject to the reinterpretations discussed above, it was found that *A. lili* settled comfortably into the *paludum* group, its character states following a congruent path to those of the other species held in this clade. The terminal clade thus formed contained an unresolved trichotomy involving *A. lili*, *A. adelaidis* and *A. paludum*. This trichotomy was resolved using the following three characters, which when added to Andersen's original (1990) character matrix (his table 1) ally *A. lili* most closely with *A. adelaidis*, forming a terminal clade with *A. paludum* as the basal sister species; the apomorphic state is given first (followed by the plesiomorphic state in parentheses):

Character 40.—Hemelytra of brachypterous form not exceeding third abdominal tergite. (Hemelytra of brachypterous form reaching sixth abdominal tergite).

Character 41.—Posterior pronotal lobe with posterior margin uniformly light colored. (Posterior pronotal lobe with posterior margin not uniformly light colored).

Character 42.—Triangular tubercle on male sternum eight large, with broad base. (Triangular tubercle on male sternum eight small, narrow).

Based on the above analysis, *A. lili* ap-

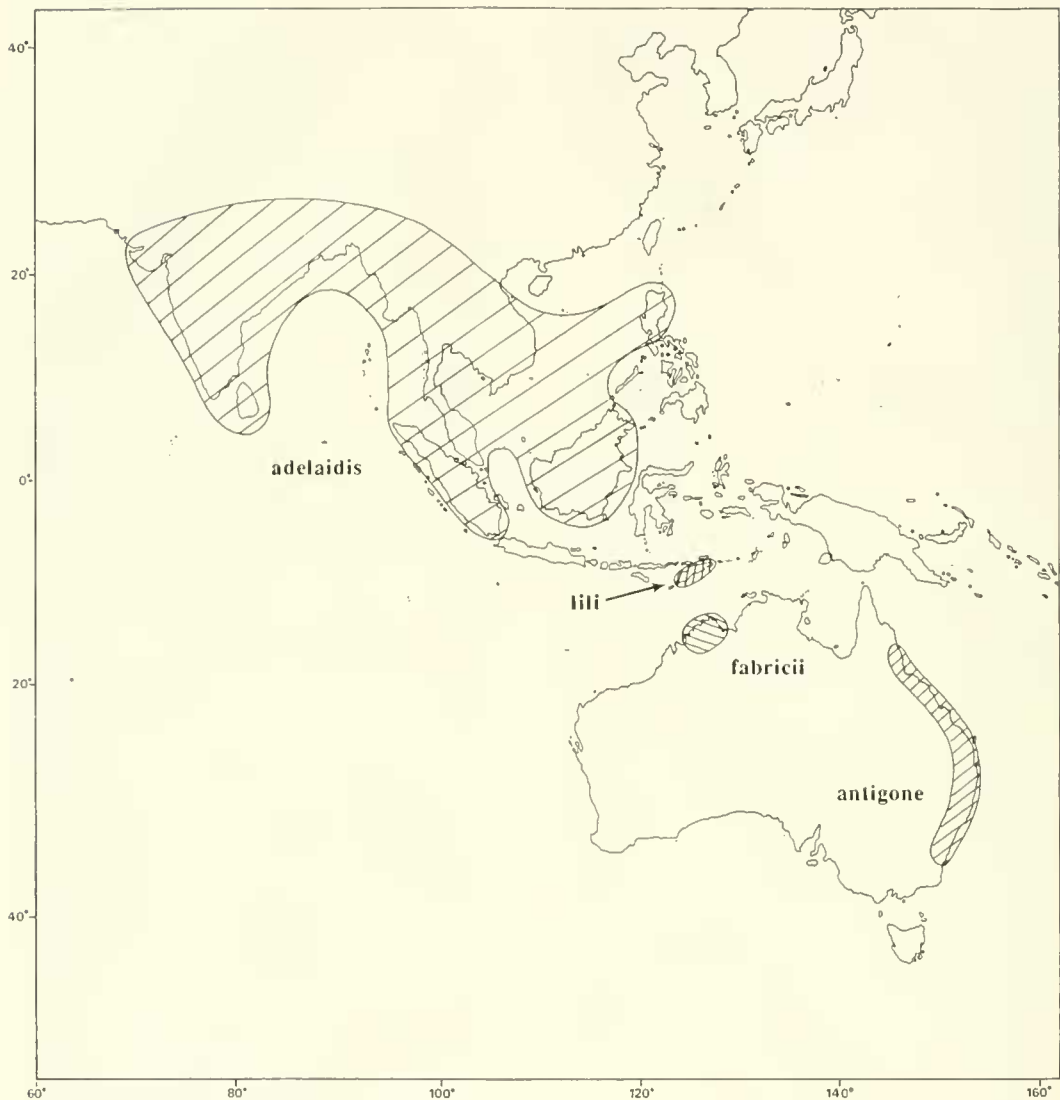


Fig. 5. Distribution of *Aquarius* species in Australia and southern Asia.

appears to be most closely related to *A. adelaidis* (Dorhn), an Asian species (Fig. 5). This pattern of relationship is shown in Fig. 6.

ZOOGEOGRAPHY

Timor lies along the southern limb of the volcanic Banda Arc, and was described by Hamilton (1979) as "tectonic chaos." The island is composed of Tertiary subduction melange with older complexes imbricated

within it, including ophiolitic and continental crystalline rocks. Most of the island is being actively uplifted, as illustrated by the presence of Quaternary reefs elevated up to 1000 meters above present sea level (Hamilton 1988). With the most southeastern location of any major island in the Malay Archipelago, Timor presently lies within 350 kilometers of the northwest coast of Australia. The two land areas were in even clos-

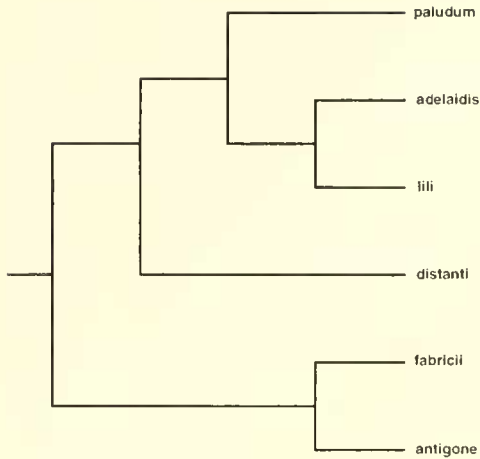


Fig. 6. Cladogram of *Aquarius* species in the *paludum* group (modified from Andersen, 1990).

er juxtaposition during the Pleistocene low sea level stands 20,000 years ago, when the Sahul Shelf, lying on the Australian platform beneath the present Timor Sea, was broadly exposed and extended subaerially to within 100 kilometers of Timor.

Both areas contain endemic *Aquarius* species, with *A. lili* n. sp. on Timor and *A. fabricii* Andersen in northwest Australia (Fig. 5), and we initially expected that these would prove to be sister species isolated on either side of the Timor Trough. However our foregoing phylogenetic analysis using the character set employed by Andersen (1990) in his revision of the genus *Aquarius* produced a species level phylogeny incorporating *A. lili* that proved this not to be the case. Based on the phylogenetic conclusions given in the previous section, *A. lili*, although indeed a member of the monophyletic *paludum* group containing both known Australian *Aquarius* species, appears to be most closely related to *A. adelaidis* (Dorhn), a species occurring in mainland Asia (India, Indochina, Malaya), the Philippines (Luzon), and the western Malay Archipelago (Sumatra, Borneo) (Fig. 5).

This pattern of relationship, shown in Fig.

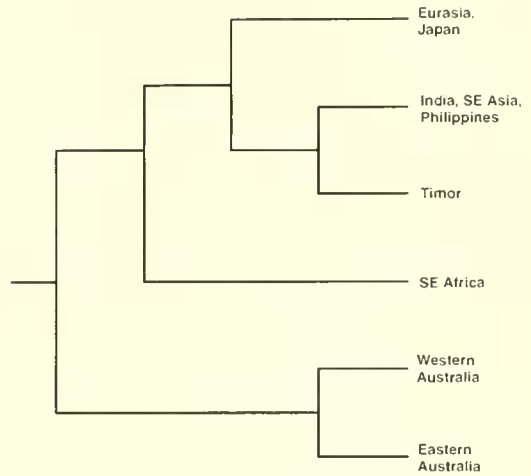


Fig. 7. Area cladogram of *Aquarius* species in the *paludum* group (modified from Andersen, 1990).

6, in turn leads to an interesting biogeographic problem. A revised area cladogram of the species in the *paludum* group is shown in Fig. 7, and indicates that the Australian areas form a discrete component distinctly separated from the remaining areas in the Palearctic Region. It thus appears that the present geographic proximity of *Aquarius* species in Timor and northwestern Australia has resulted from the northward drift of Australia and its incipient collision with the southeastward migrating Banda Arc. This analysis further indicates that the Australian species are not the result of a recent colonization by Asian stocks via stepping stone dispersal along the present Banda Arc, nor has the Timorese species been derived via dispersal of Australian stocks onto the advancing Banda Arc. Instead, the separation of these lineages reflects a series of much older and more fundamental isolation events. These could have occurred as long distance dispersals at some point in the distant past, but are just as likely to represent vicariance due to tectonic continental fragmentation in the Mesozoic.

The fact that *A. lili* is not sister to any Australian *Aquarius* species has important

bearing on two currently advanced hypotheses regarding the geological evolution of Timor. The first hypothesis, discussed extensively by Hamilton (1979) and referred to subsequently as the fore-arc ridge hypothesis, maintains that Timor is the exposed crest of the Banda Arc fore-arc ridge which has been ramped onto the Australian plate margin. A second hypothesis, strongly supported by Audley-Charles (1986) and referred to herein as the continental margin hypothesis, interprets Timor as being the deformed edge of the Australian continental plate that has ridden over the Banda subduction zone.

The two hypotheses offer alternative biogeographic scenarios. In the fore-arc ridge hypothesis, Timor is composed of fragments of the Banda Arc system that have migrated southeastward from an original position nearer Borneo and Celebes. This would have allowed Asian faunal elements to have been tectonically rafted into closer juxtaposition with Australia (although it also permits the possibility of dispersal from an Asian source area onto the migrating arc at any time during its history). In the continental margin hypothesis, Timor is composed of uplifted Australian plate basement and overlying sediments that were elevated in an oceanic setting and had no previous land connections, and any Asian elements occupying it would have arrived via long distance overwater dispersal only. The fore-arc ridge hypothesis is thus one that could invoke vicariance, dispersal, or a combination of the two, while the continental margin hypothesis allows only for the possibility of dispersal.

The present area relationships of *Aquarius* species seem to support the fore-arc ridge hypothesis most strongly. The presence of an Asian derived *Aquarius* species on Timor is anomalous in light of the fact that no known intervening populations occur on Celebes, the Moluccas, or the Lesser Sunda Islands, where extensive aquatic Heterop-

tera surveys have been undertaken. Had the ancestor of the Timorese *Aquarius* species dispersed eastward through the archipelago it would seem likely to have left other populations in its wake in these areas. This suggests that the disjunct pattern involving *A. lili* may have been established by vicariance prior to the present configuration of these islands, possibly by tectonic rafting on continuously subaerial fragments within the southeastward migrating Banda Arc or a precursor, as suggested above. Although Timor is primarily composed of marine limestones and clays, it has incorporated within it fragments of continental and ophiolitic rocks that may have been transported over great distances from an Asian source area. Hamilton (1979) hypothesized that the Banda Arc had migrated eastward in the Miocene away from a position near medial Celebes, which at that time formed the eastern margin of the Asian continent. This tectonic rafting scenario is further supported by the record of an Eocene fossil anthracothere (a hippopotamus relative) of Southeast Asian affinities from central Timor (von Koenigswald 1967). This fossil represents a full sized species, unlike the Pleistocene pygmy stegodont proboscidiens known from Java, Celebes, Flores, and Timor (Hooijer 1970, Audley-Charles and Hooijer 1973), and thus does not appear to have arrived via overwater dispersal.

Another consideration involves the proximity of potential source areas from which dispersing ancestors could have arrived. As discussed above, if the continental margin hypothesis is accepted, then the ancestor of *A. lili* would need to have arrived overwater, since the uplifted continental margin would have had no land connections to the Banda Arc islands to the north, and would have been separated from the exposed Pleistocene Sahul Shelf by the Timor Trough. Based on geographical proximity and prevailing wind regimes, however, such dispersal would seem more likely to originate from

nearby northwestern Australia rather than from more distant populations in the western Malay Archipelago, a pattern not supported by the cladistic evidence.

These lines of reasoning do not prove or refute either geological scenario, but do seem to lend greater support to the fore-arc ridge hypothesis. Timor contains additional unusual elements in its aquatic Heteroptera fauna, and ongoing studies may provide further evidence bearing upon such geological and zoogeographical problems. For example, a preliminary phylogenetic analysis of the gerrid genus *Ptilomera* indicates that the morphologically aberrant Timorese representative, *P. timorensis* Hungerford and Matsuda, is most closely related to species occurring on the Asian mainland and the Greater Sunda islands rather than to species occurring on the nearby Lesser Sunda islands of Sumbawa, Flores and Sumba. Timor thus remains an anomalous island within the Malay Archipelago, and zoogeographic studies of its aquatic Heteroptera fauna hold the promise of further independent evidence regarding the island's tectonic evolution.

#### ACKNOWLEDGMENTS

We are pleased to acknowledge the invaluable assistance of the following persons who aided us with permits, guidance, transportation and logistics, and without whose help and patience our field surveys in Timor could not have been accomplished: Drs. Rosichon Ubaidillah, Dr. Soetikno Wiroatmodjo, Dr. Mohammed Amir, and other personnel from the Indonesian Institute of Sciences (LIPI), Bogor; Mrs. Moertini, Mr. Sanchoyo, the other staff members of the LIPI office in Jakarta; and most particularly Waldemar Hasiholan, Jous Laiskodath and R. I. Petrusz, Ministry of Forestry, Timor.

We also thank Dr. Warren Hamilton of the U.S. Geological Survey, Denver, Col-

orado, for reviewing the geological discussion and suggesting improvements.

The holotype of *Aquarius lili* is deposited in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); paratypes are held in the J. T. Polhemus collection, Englewood, Colorado (JTPC), the Bishop Museum, Honolulu, Hawaii (BPBM), and the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB).

This research was sponsored by a series of grants (2698-83, 3053-85, 4537-91) from the National Geographic Society, Washington, D.C., and by grant BSR-9020442 from the National Science Foundation, Washington, D.C. We thank these organizations for their continued support on research into the systematics and zoogeography of aquatic Heteroptera.

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Appendix 1. Coding of character states for *A. lili*. See Andersen (1990, table 1) for explanation of characters and character state codings.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0
21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	
0	1	1	0	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	